Research Article

Application of stochastic and linear models to the assessment of a population's genetic structure stability and selection event duration: The study of Pucciniagraministritici stem rust

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ABSTRACT
The aim of the research is modeling the strength of natural selection on a population. In this context, "physical selection" (decrease in a form's occurrence rate down to elimination) is considered to be the result of chaotic oscillations of the occurrence. The latter include 1) "stochastic physical selection" (recurrent extinction of a form due to random oscillations), which is predicted by the Goodman-Belovsky birth and death model, and 2) "directional physical selection" (gradual changes in the occurrence rate) described by the linear regression equation. The two models were verified using the data on the occurrence rates of different races within the macropopulation of stem rust (*Pucciniagraminis*) in the United States. The extinction tolerance varied significantly (by a factor of hundreds) among the races which were present in the same population at the same time. Statistical lifespan expectations of the races were relatively equal to the observed lifespans only in case of small slope values of the linear regression. The prevalence of the "stochastic selection" over the "directional selection" in most races could be caused by instability of the anthropogenic environment of the stem rust populations.

Keywords: quantitative genetics, natural selection, model of microevolution, relative fitness, adaptive value, *Pucciniagraminis*

INTRODUCTION

The classical models of Wright and Fisher's population genetics have been repeatedly criticized for being based on unrealistic assumptions. For instance, S. V. Chudov (2002) in his mathematical review of the criticisms summarizes the following drawbacks of the models. Thespatial structure of populations is neglected; the exponential growth model is used, which is only relevant under non-competitve conditions; the nonzero stationary solutions do not apply to this model. There is no doubt that the authors of the models understood all that, but they aimed to validate particular statements of the evolutionary theory of their time, rather than to create a universal theory of the phenomenon. Therefore, inherently simplified presumptions were made.We consider important the fact that, in case of natural microevolution, more or less chaotic oscillations are observed more often than steady decrease or increase in the occurrence rates of different forms predicted by classical models. The fluctuations of color forms occurrence in the population of the two-spot ladybird (*Adaliabipunctata*), discovered by Timofeev-Resovskii (Zakharov1992), are a good example. There is another classic example – the shift of balance between light and dark-colored morphs of the peppered moth (*Bistonbetularia*) in the British Isles due to industrial pollution. It is intriguing that, in the latter case, there was an increase in the numbers of light-colored peppered moths when the level of air pollution became lower again (Grant et al. 1995). Therefore, such changes in the occurrence rate are reversi-

ble and cannot be considered natural selection as such. It is more correct to regard elimination of a form, rather than mere changes in its occurrence, as a selection event. And it is elimination of a form that should be the object for modeling. Apparently, it is no use describing the oscillatory processes with monotonous models. Classic models can definitely be applied to the simplest cases, but "the simplest case" is not necessarily equal to "the usual case".

The presence of several forms in a population is called balanced polymorphism. Yet, balance can be both stable and unstable, with different results. Therefore, the possibility of an elementary selection event within a completely or almost completely isolated population should be determined by how well-balanced the polymorphism is (in the sense of sustainable existence of all its forms) and what the probability of balance disruption (extinction of one or several forms) is under particular conditions. The occurrence rate oscillations, sometimes leading to elimination, are apparently caused by environmental factors with an unknown or even absent scenario of changes in each particular case. The implementation of the probabilistic approach naturally suggests itself in this situation.

The currently existing stochastic models of evolution are based on the famous Kolmogorov equations, which are known in physics as Fokker–Planck equations. They use more realistic presumptions, particularly, the finite size of a population. For instance, attempts were made to model the changes in the range of allele frequencies in the gene pools of human populations (Evans et al. 2006). However, the probability of an evolutionary event is the parameter which is sometimes not applicable. In genomics, where large numbers of nucleotide replacements are studied, the average probability of a replacement can be defined. Yet, the probability of a single nucleotide replacement can significantly differ from the average value.In field biology, we deal with polymorphic populations, which are more often characterized by a ratio of several separate forms, rather than by a frequency spectrum of a large number of features. Therefore, to make our model verifiable, it is more interesting to learn how to calculate the lifespans of particular

forms, as this parameter can be observed empirically. The Kolmogorov backward equation provides a theoretical opportunity to calculate the lifespan of a morph under natural conditions, but it is based on the relative fitness of competing species, which is hard to determine and time-inconsistent.Thus, successful implementation of the Kolmogorov equations in predicting the duration of real population processes is possible in cases of "neutral evolution", when relative fitness of different forms is a priori considered equal. For instance, the "mitochondrial clock" methods are based on the presumption that most mutations are neutral and occur at a uniform rate (O'Connell1995). When we can check the "clock" through historic data, we observe significant discrepancy and have to "calibrate the clock" (Gibbons1998). Therefore, as one would expect, the process of nucleotide replacement is not exactly random, as the differences in adaptiveness have their impact.Since Darwin, an evolutionary act has been commonly considered a result of stability loss by the ancestral form. However, if the original form loses its stability, it means that the population has several forms, each characterized by its own stability. Then, the fitness (the ability to produce offspring) variations among the forms, competing within a population, should find physical expression in the stability variation of these forms.

Therefore, rather than fitness or selection coefficient, it is better to choose the stability of a form, which is tightly connected to the integral impact of environmental factors and to the lifespan of the form, to be the main characteristic of the future of the form. Over the last years, fairly complex models with multiple parameters have been developed to calculate the survival of populations of living organisms (Pierson et al. 2014). These models require the examination of heterozygosity, chromosomes, reproductive success, and other complicated studies. Unfortunately, the authors of the models do not consider the stability of a form within the population.The stability of a population's genetic structure was studied by N. V. Timofeev-Resovskii and Yu. M. Svirezhev (1967). These researchers chose to model all the possible situations separately: the selection of recessive or dominant genes, in-

complete dominance etc. However, we are often unable to understand the kind of genetic determinacy of a feature during the analysis of natural populations. Thus, the existing models of natural selection share a common disadvantage: they are based on the characteristics which are not stable enough and are hard to determine.

RESEARCH METHODS

It is generally better to assess the stability of a form through the behavior of this form, i.e. through the parameters of its occurrence oscillations. At a first glance, the solution seems to be simple – the higher the range of the occurrence oscillations of the form is, the less its stability is. If the occurrence oscillations were determined by random combinations of environmental factors alone, the stochastic model would be able to provide rather precise estimation of the probability of any system state, including extinction (the numbers of a form reaching zero). However, it should be remembered that a directional trend caused by unequal fitness of competing forms should manifest itself against the background of a stochastic process. Therefore, we have to apply a stochastic model to the process which is not fully stochastic. Thus, during the analysis of empirical data, we deem it reasonable to model the observed oscillations as a random process and to consider the trend a systematic error which can be estimated by an additional linear regression model.

We found the modified model of birth and death, extensively described by D. Goodman (1987), to meet our requirements for the stochastic model. This model defines a functional relationship between the actual absolute numbers of a population at the moment of assessment and the statistical expectation of its lifespan. Therefore, if we observed extinction of a population while monitoring its numbers, we can check the probability of the discrepancy between the observed lifespan of the population and the statistical expectation "predicted" by the model. In our case, the model is applied to separate forms within the population, rather than to the population as a whole, so "good" lifespan predictions for several forms that become ex-

tinct (or almost extinct) during observation generally prove the high quality of the model.

The equation of the model is as follows.

$$T(N) = \sum_{x=1}^{N} \sum_{y=x}^{N_m} \frac{2}{y \, (y \, V(y) - r(y))} \prod_{z=x}^{y-1} \frac{z \, V(z) + r(z)}{z \, V(z) - r(z)}$$

, where

$T(N)$ isstatistical expectation of a population's lifespan;

N is numbers of the population at the "initial" moment of the lifespan;

N_m (maximum possible) is extreme numbers of the population (usually much higher than the ecological capacity of the environment);

$r(n)$ is statistical expectation of per-capita rate of increase at n population numbers;

$V(n)$ is dispersion of per-capita rate of increase at n population numbers;

z is population numbers from x to y-1 (the multiplication index in the formula), y is the summing indexfrom y = x to N^M.

It should be noted that, according to the model design, for each $1 \le n \le N_m$ the expression $V(n) > r(n)$ should be true. Otherwise, the values of $y \, V(y) - r(y)$ and $z \, V(z) - r(z)$ may become zero or fall near the zero point, leading to an artifact. That is why in case of constant (for instance, averaged) values of the increase rate and its dispersion $r(n) = const = \bar{r}$ and $V(n) = const = \bar{V}$ (this is the case we will be considering below) the expression $|\bar{r}| \ll \bar{V}$ should be true for higher reliability.

The authors of the model applied it to assess the lifespan of the island populations of northern mammals in the upper belts of the Rocky Mountains, USA, where these populations are the Pleistocene relics. In many cases, the results were similar to their separation times obtained from the paleoclimate data (Belovsky 1987). Therefore, the model is tentatively functional.

The statistical expectation calculated by this model is the expected number of generations before the numbers of the form reduce to zero with 95% probability. We suggest, using this characteristic, to perform a comparative analysis

of the stability of forms within a polymorphic population.

The stochastic model is based on the null hypothesis, which will be true, if there is no directional physical selection. On the contrary, the linear model of the population numbers growth or decrease, based on statistically stable coefficients of linear regression, describes the other extreme situation, when the numbers of the population change with perfect regularity, according to the regular linear law, and random oscillations are not really present. It is obvious that the truth is somewhere in the middle.

We used the estimation of expectation for physical selection as a linear model, having developed parametric linear regression based on the temporal series of absolute numbers. The validity of the latter was assessed through Fisher's F-test. This criterion reflects the probability of equality between the dispersion of the series members around the regression line and their dispersion around mean value (obviously, the less the difference is, the more accurate the regression is). The absolute value and the sign of the slope of this regression will reflect the mean value and the sign of the directional physical selection, respectively. The following parameters were calculated: B — the slope of the regression, C — the intercept, and F — F-test statistics, percentage.

In this paper, we mean physical selection to be the change in the absolute numbers of a form (contrary to the existing "metaphysical" definition of selection as the combination of causes changing the occurrence, used, for example, by N. H. Barton and M. Turelli (1989): "changes in the means and variances that are caused by directional and stabilizing selection".We characterize the rate of this selection by the absolute value and the sign of the changes in the numbers of the form. We call directional physical selection the statistically stable increase or decrease in the numbers of the form. We call stochastic physical selection the observed elimination of the form due to the random (unpredictable) oscillation in numbers, describing it through the rate or the number of generations.

Both models do not require any abstract coefficients to be "tried" or "guessed", they are based on the values, which can be directly measured or, at least, indirectly estimated. We will try to assess the parts of directional selection and random fluctuations in the observed changes in the abundance of forms, comparing the "predictions" made by two models; then we will try to estimate probable timescales of their extinction, based on these data.We apply absolute values, as abundant forms are generally more stable than those small in numbers. Under natural conditions, researchers usually determine relative characteristics: population density rather than numbers, or abundance of the form examined. However, relative values are hardly suitable for the assessment of stability. For example, a certain form may account for a tiny fraction of one per cent of total the numbers of a population, while its absolute numbers equal to thousands of individuals.It should be noted that we faced certain difficulties transferring the Goodman model from ecology to population genetics. The studies on population genetics include rather precise measurement of relative numbers and quite rough estimates of absolute numbers. As noted above, we required the absolute numbers. Surely, it is possible to determine the maximum possible or the initial numbers of a small relic population with enough precision, but the conditions are not always so favorable. Therefore, we have to learn to make this assessment based on the known relative numbers or on the biological knowledge about particular objects.In the case described below we managed to estimate the maximum possible numbers of a population according to records. However, the figure turned out to be so large, that the computing power of the Russian Academy of Sciences' supercomputer was not sufficient to run the stochastic model, so we had to take lesser values of Nm and determine the maximum values approximately through geometric extrapolation.

MATERIALS AND INPUT DATA OF THE MODEL

The races of the *Pucciniagraminis* stem rust, whose long-term occurrence dynamics is described by Dobzhansky (1970), were chosen as test objects for the models. Stem rust is a serious wheat blast in the United States. It was exten-

sively controlled during the 1920s and the 1930s, both through the elimination of intermediate hosts and the selection of resistant varieties of wheat. These measures resulted in the emergence of new stem rust races, which were tolerant to certain control methods. The table provided by Dobzhansky(Table 1) shows that during the 1930s the occurrence of different stem rust races within the U.S. territory was oscillating, mostly in a seemingly chaotic mode. Such pattern is quite in line with the situation discussed above and is, probably, caused by the influence of, at least, two statistically independent selection factors – the expansion of the resistant varieties of wheat and the elimination of the stem rust intermediate host – barberry.

Table 1 Occurrence rates (percentages) of stem rust physiological races in the USA (Dobzhansky 1970). Highlighted are the races that became "extinct" during observation. Among them, race 34 was not registered in 1941 but reappeared in 1942 in far larger numbers. Race 11, similarly "extinct" in 1944, re-emerged in the end of the 1940s.

Годы	№11	№17	№19	№21	№34	№36	№38	№49	№56
1930	4	0.3	0.6	6.7	0.6	36	30	20	0.2
1931	22	0.6	1.3	4	2.1	28	15	25	1
1932	4.9	1.4	4.9	1.6	0.9	9.6	46	27	2.1
1933	1.7	1.4	1.4	4.5	7.1	3.7	33	37	3.7
1934	0.6	0.6	0.3	1.8	22	21	2.8	1.3	33
1935	19	1.5	1.3	7.4	18	6.1	4.6	1.4	44
1936	12	4.4	1.2	0.8	4.2	3	22	1.2	47
1937	8.4	6.1	3.1	0.6	1.1	6	8.7	7.4	56
1938	2	3	6.4	1	0.8	1.2	16	0.9	66
1939	3.2	10	3.3	0.4	0.6	0.8	24	0.6	56
1940	4.2	34	2.2		0.5	1.8	10	1.2	44
1941	1.3	51	3.8			2.5	6	2.4	32
1942	0.3	27	6.2			2.3	27.3	3.9	31
1943	0.1	23	1.9			0.4	24.4	0.3	49
1944		21	6.6			0.2	26.1	0.2	43

According to the existing records (Flyaksberger 1935; Yakubtsiner 1955), in 1934-1938 the yield of wheat in the USA equaled 194.760 m centner per year. Considering a centner consists of an average of 3 m grains, and a wheat ear contains an average of 50 grains, we estimated the total amount of wheat in the US to be $1.16856 \cdot 10^{13}$ (11685.6 billion) plants. The size of population of an organism which reproduces through airborne spores should be the same as the size of its geographic range, therefore, the maximum size of the stem rust population should be of the same order, i.e., 10^{13}. Stem rust produces several asexual generations a year, but the sexual process, which can significantly change allele occurrence, takes place once a year. Therefore, we equaled one generation to one year, which slightly decreases the accuracy. A number of papers prove that the populations of species with intense gene flow almost match the geographic range of the species (Yuriev 1997). It should also be true in case of stem rust. This fact simplified the model testing. The calculations by the modified birth and death model were performed with the help of a program written in IBM XL Fortran programming language using the parallel programming library of the MPI standard. The resources of the Joint Supercomputer Center of the Russian Academy of Sciences provided the opportunity to calculate $T(N) | N_m$ for different values of the maximum size of the population up to $N_m = 10^7$. The rest of the calculations were performed via Microsoft® Excel 2003 spreadsheet, which was also used for graph plotting.

The parameters of the modified birth and death model and of the linear model – the regression of the relative race numbers $\eta_{1930+i-1}$ for the first members of natural sequence – were identi-

fied for each race based on the temporal series (see Table 2).

RESULTS

Our studies led to the following results. The expected lifespans of the races monotonically increase with increasing maximum size of the population, which is represented in Fig. 1. Moreover, if we specify the linear scale of the time axis (T) and the logarithmic scale of the numbers axis (N_m), the resulting function turns out to be almost linear at rather high values of N_m, which provides the possibility of extrapolation to even higher values.

FIGURE 1 ABOUT HERE

Our results suggest that the calculated values of the expected maximum lifespan of the stem rust races within the macropopulation vary over a wide range. Generally, we can separate the races with high, low and moderate stability. However, the estimates from the stochastic model are not equally precise for all the races, as the results from the linear model suggest that certain races undergo directional selection, thus being not completely "stochastic". Therefore, we will use the "predictions" of both models.

Table 2 $\bar{r}$,$\bar{V}$, B, C and F parameters calculated for the races. Highlighted are the races that became "extinct" during observation.

	№11	№17	№19	№21	№34	№36	№38	№49	№56
$\bar{r}$	2.34	0.686	0.762	0.249	0.854	0.147	0.576	0.357	1.02
$\bar{V}$	74.5	1.12	1.90	1.87	5.83	2.12	2.30	2.33	5.11
B	-0.760	2.58	0.274	-0.535	-0.333	-1.88	-0.421	-1.94	3.29
C	11.7	-8.26	0.778	5.82	7.26	23.2	23.1	24.2	7.54
F	2.96	0.000596	0.127	1.71	98.9	0.000372	97.5	0.00197	0.00809

Race 17 is in the lead within the high stability group. The results of the extrapolation show that its expected lifespan within the macropopulation coming up to 10^{13} is more than 5 thousand years, due to the combination of moderate increase rate and low dispersion. However, this is the race influenced by intense and, statistically, quite stable positive directional selection($B= 2.58$; $F = 0.000596\%$), providing significant deviation from stochastic behavior (see Table 2 above). Therefore, in this case the "prediction" of the stochastic model is considerably overstated.

Race 19 is also highly stable, undergoing positive directional selection, which is one order less intense (linear regression of 0.27) than the one for race 17. Despite this fact, the stochastic model predicts remarkable expected lifespan (~128 years), also due to not so high per-capita rate of increase and low dispersion, which is, however, markedly higher than the one of race 17 ($B = 0.274$; $F = 0.127\%$). In this case, we observe not just a stable, but almost steady state with slowly increasing absolute numbers, undergoing minor oscillations. Perhaps, this is the state which should be considered the most favorable in terms of a form's survival.Races 38, 21, 49 and 36 have moderate stability (expected lifespans are ~ 50, 41, 37 and 32 years, respectively). Race 38 does not undergo any statistically stable directional selection ($B = -0.421$; $F = 97.5\%$). The increase rate of this race is just a little lower than those of stable races, but it varies more significantly over the years ($\bar{r} = 0.576$; $\bar{V} = 2.30$), providing slow increase in the expected lifespan with the increase in maximum possible size of the population. Such state of a form is probably steady.Next, races 21, 36 and 49 have stably negative values of the selection coefficient ($B= -0.535$; $F = 1.71\%$;$B = -1.88$; $F = 0.000372\%$ and$B = -1.94$; $F = 0.00197\%$, respectively). Their increase rates are 2-4 times lower than those of the stable races, while the dispersions of the increase rates are slightly higher (up to 2 times). Race 21 has the smallest absolute value of the selection coefficient, which is also statistically the least stable. Therefore, both the stochastic and the linear models predict that race 21 should be slightly more stable than the other two races, and still it became "extinct" during the observation period. However, the numbers of all three races reached very low values during the period of observations. Apparently, the "extinction" of races 36 and 49 is also quite probable.

Finally, the stochastic model "predicts" races 56, 34 and 11 to be the least stable (expected lifespans are ~18, 17 and 2 years, respectively). At the same time, race 56 undergoes statistically stable and intense positive directional selection ($B = 3.29$; $F = 0.00809\%$), which is absent in case of race 34 ($B = -0.333$; $F = 98.9\%$), while race 11, on the contrary, undergoes minor, not so stable, but still detectable negative directional selection ($B = -0.760$; $F = 2.96\%$). The increase rates, as well as the dispersions of the increase rates of these races, are several times higher than those of the races with moderate stability. It is not surprising that races 34 and 11 became "extinct" over the observation period. It should be noted that the "extinction" of race 34 was the result of random fluctuations of its numbers. Consequently, we might say that in case of race 11 the stably negative selection and random oscillations of the numbers had combined influence. To avoidany doubt, we should note that the random factor was, in fact, counteracting the regular one, that resulted in spontaneous rise in numbers in 1931 and 1935, which were, actually, expectable in the context of rather high values and high dispersion of the increase rate of race 11 ($\bar{r} = 2.34$; $\bar{V} = 74.5$).

DISCUSSION

It can be tentatively concluded that the selected pair of models works adequately, allowing to reveal substantial features of changes in the numbers of different forms for further comparing. Two facts are of interest.First, the "stochastic selection" clearly prevails over the "directional selection".Second, the races coexisting within the same population have extremely different expected lifespans.

Even if we consider the "predictions" of the stochastic model alone, without revealing the patterns of directional changes in numbers, it can be noticed that during the observation period two of the three races, which have been identified as "unstable", became extinct, while in case of the four races which have been considered "moderately stable", only one of them became extinct. This fact is in agreement with the initial assumption that, at least in case of no intense directional physical selection, the "predictions"

of stochastic model can provide adequate assessment of a form's stability. Therefore, "stochastic selection" has generally more impact on the extinction of races than "directional selection". Our results confirm the earlier conclusion by P. L'Heritier and G. Teissier (1933) that negative directional selection is inefficient compared to stochastic selection, which is able, in case of general depression of the population, to "wipe out" the last carriers of the respective genes.

In theory, it is possible to get much more precise predictions based on the stochastic model, if we calculate the increase rate and its dispersion with respect to the regression line rather than the X-axis. Apparently, in this case the increase rate will generally be lower than the initial one, and the dispersion will decrease, as well. Then the result could be considered the most closely approximated to the absence of directional physical selection. It would be possible to compare the relative influence of directional and stochastic selection on the lifespan of a form. However, even without this sort of detailing, the results appear to be reasonable, despite the small duration of the observation sequence and the reliability of the input data being far from perfect.

Basically, in several dozens of generations the population should be narrowed to one or several most stable forms. In case of the examined stem rust macropopulation, the duration of this "stabilization" should hypothetically be equal to ~128 years ("generations"), as this is the period of 95% probability of extinction for all the races but the most stable one, race 17.However, this estimation does not consider the latent, for example, heterozygous existence of races, mutations, which may lead to the emergence of new races, and any other possible changes in the situation, which are able to generate directional physical selection. Furthermore, there is interracial competition; therefore, the extinction of one, not to say several of the races, should also have impact on the stability of the remaining ones.The appearance of new races of stem rust can hardly be considered speciation. But does the model provide an opportunity to detect early stages of speciation? If any of the forms somehow become genetically isolated, its increase rate and the dispersion of the latter will probably

not be significantly different from those at a non-isolated state. We may expect some reaction of the model only if the emerging species gains new ecological properties, such as the ability to use some new resources. M. Shaffer (1987) distinguished three types of uncertainty within the birth and death model: demographic, environmental and catastrophic. The dependence of the expected lifespan on the size of the population should be different for each of the types.

The linear chartsdemonstrating the dependence of stability on the size of population correspond to the environmental uncertainty, as it was expected. On the contrary, a new species will, probably, not be demographically stable at first: one has only to think about the reproduction of rabbits brought to Australia and other examples of new species introduced into natural communities. In this case the correlation between the increase rate and the actual size of the population will be exponential, typical for the initial periods of population growth in the presence of abundant resources.Our method did not detect speciation in stem rust.Even Darwin noted that evolutionary events are connected with the loss of stability and emergence of "abnormal" phenotypes (Schmalgausen 1969). In case of weaker stabilizing selection, the expected lifespans would be similar in different races.

There are two factors complicating the modeling. First, the stochastic model "predicts" the numbers of the race reducing to zero, not the absence of individualsthat would be able to generate the race through breeding. Second, the empirical numbers of a race were defined as zero, when observers were not able to detect it anymore. In 1941 race 34 became "extinct", "resurrecting" the next year, while race 11, which became "extinct" in 1944, reappeared in late 1940s after the Barberry Eradication Program in the USA (Roelfs et al. 1991). This is why we enclose the words "predict" and "extinct" in quotation marks.The point is that, unlike most other races of stem rust, race 11 is able to thrive on other intermediate hosts than barberry, thus, when people cleared the place occupied by other races, it rose in numbers and achieved remarkable levels once again. This fact proves the existence of competitive relationships between the races.However, the "predictions" of the stochas-

tic model expectedly seem to be inadequate for those particular races which, according to the linear model, undergo significant directional physical selection.The second essentially weak point of the model is the underlying principle of actualism. We imply that the conditions will always be more or less the same, as they have been during the time period of initial data collection. The model does not take account of future mass campaigns for barberry eradication, global climate changes, and other exclusive events, which may change the relative adaptability of forms. However, strictly speaking, the stochastic model considers all the events that influence the competitiveness of studied objects to be random, differing only in their occurrence rate and in the correlation between this rate and the duration of observations.In this context, one should distinguish between relevant and irrelevant events, having in mind that with increasing period of monitoring, more and more irrelevant events should be considered relevant. For instance, when it comes to Russia, an abnormally torrid or rainy summer takes place once in a few years, summer floods, overwhelming the whole floodplain – once in 15 years, a hurricane, destroying log houses – every 70-150 years (Borisenkov and Pasetskii 1983). If future generations have data from genetic monitoring covering several centuries, these events will be relevant, having regular impact on the increase of the occurrence rates of the observed forms, their dispersion, expected stability of phenes and so on.Another possible complication is that input data are not always uniform. Since the experiments of L'Heritier and Teissier, the correlation between directional natural selection and population density has been established. In these experiments, the occurrence rate of the eliminated characteristic did not reduce to zero, stabilizing at a very low level and oscillating around it for a long period. We observe a similar pattern in case of races 11 and 21. In 1934, a new variety of wheat was introduced in the USA, which was highly resistant to these races, leading to rapid decrease in their occurrence rate. Therefore, the stability of races 21 and 11 was calculated from non-uniform data, first collected in the context of high occurrence rates, then of low ones. Apparently, "stepwise" increase rates of races and

their dispersions will be different in case of low occurrence rates. The increase rate dispersion turns out to be overestimated, and the stochastic model reacts to drastic decrease in the race occurrence by predicting short lifespan.

Perhaps, this is the reason for race 11 to outlive its expected lifespan by 7 times. Similar problems may occur in case of rapid increase in the occurrence rate, as it happened in case of race 56.However, it is easy to track such cases with the help of the linear model, revealing the presence of statistically stable directional selection. In order to obtain more precise results, one should examine the data for high and very low occurrence rates separately.Unlike competing species, different forms of the same species within a single population not only interfere with each other, but are also able to help each other survive under adverse conditions in heterozygous state. Indeed, it cannot be ruled out that restoration of race 11 was not only due to a small number of individuals of corresponding phenotype, but also due to segregation of the phenotype during the crossing of other races of the fungus.If gene flows within a macropopulation are relatively slow, its spatial structure becomes important. Let us assume that we have the same network of observers and confine ourselves to the same assessment procedure. Then the increase rates of the absolute numbers of the forms can be different at all locations, being on average lower than in the panmixis situation, as a result of spatial barriers obstructing the expansion of particular forms. Therefore, in this case, the "predictions" of the stochastic model should give us overestimated lifespans of particular forms and, accordingly, overestimated expected duration of an elementary selection event. In this case, the data from each observation point should be analyzed separately, as the average values for the whole macropopulation lack physical sense.

What is the relevance of the proposed method? We gain the knowledge of macroevolution with the help of paleontology, comparative anatomy and molecular systematics. The information on microevolution is mostly obtained from experimental data and, partially, from long-term"temporal" observations of natural populations, such as the examples given above. The assessment of the stability of any forms within any populations will allow quantitative comparison of selection under experimental and natural conditions, within the populations of the same species under different conditions, in cases of interspecies competition and, in some cases, even in the existing and extinct populations. Such data will provide an opportunity to reveal the patterns of natural selection. The presence of certain patterns is evident, for instance, from the existence of homologous series. Undoubtedly, the data of this kind will be included in future theories of evolution.

CONCLUSIONS

1. The attempt of simultaneous implementation of two models, describing antithetical cases, when the numbers of genetic races change due to random fluctuations alone and solely due to the impact of stable directional selection, has demonstrated the opportunity to make qualitative conclusions about the origins of the observed changes from the temporal series of the numbers of races.

2. Within a large population which is almost matching the geographic range of the species, the stability of phenes, races or biotypes can vary by a factor of hundreds. Therefore, an elementary selection event can take place even in the absence of directional physical selection due to marked differences in the statistical stability of the forms.

3. The stochastic model provides an opportunity to assess the duration of an elementary selection event and to predict the outcome of competitive struggle, but it does not account for the existence of stable directional physical selection and drastic changes in environmental conditions. Therefore, the result we obtained in our example – the stabilization of physiological race 17 in 128 years with a probability of 95% – is just a rough estimation of the evolutionary capacities of the stem rust population during the period of 1930s, rather than a "prediction". In order to get more realistic predictions, one should calculate the increase rate and its dispersion with respect to the regression line rather than the X-axis.

4. The prediction feasibility can be improved by increased duration and sampling of observations. However, it will require additional formal techniques, which canfacilitate revealing the spatial structure of a population.

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Fig. 1 Expected maximal lifespans of stem rust races depending on maximal population sizes.
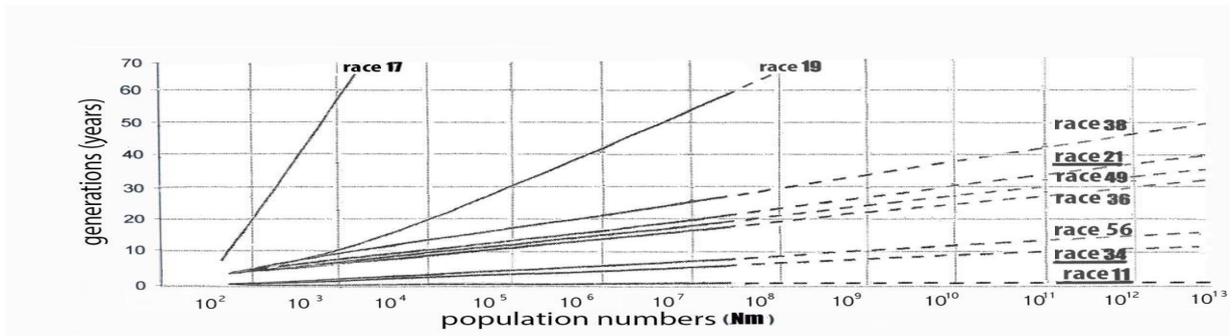
Underlined are the races that became "extinct" during observation.